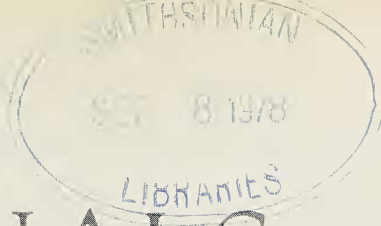


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## TAXONOMIC AND KARYOLOGIC COMMENTS ON SMALL BROWN BATS, GENUS *EPTESICUS*, FROM SOUTH AMERICA

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### ABSTRACT

The South American species, *Eptesicus brasiliensis* (Desmarest), *E. furinalis* (D'Orbigny), and *E. diminutus* Osgood, were investigated in order to identify a collection of *Eptesicus* from Tucumán and Catamarca provinces, Argentina. The name *E. dorianus* (Dobson) cannot be applied to any of the known taxa, and is treated as a *nomen dubium*. All three species appear to be strongly dimorphic in size, with females being larger than males. The three species form a size continuum, with *E. diminutus* being the smallest species and *E. brasiliensis* being the largest. Some size overlap occurs between *E. furinalis* and the other species, but this usually involves males of the larger species and females of the smaller species. This size overlap has given rise to the misidentification of some specimens by previous workers, and has resulted in the mischaracterization of *E. diminutus*. Samples of a population of *E. furinalis* from Tucumán Province and adjacent areas in northwestern Argentina are larger than other known populations, and also differ in other details. This population is named as a new subspecies. The karyotypes of *E. furinalis* and *E. diminutus* are identical in appearance, and exhibit the same structure as other New World *Eptesicus*. The 50 chromosomes consist of 24 pairs of acrocentric autosomes, grading from large to small, a large submetacentric X chromosome, and a small acrocentric Y chromosome.

### INTRODUCTION

The genus *Eptesicus* is represented in South America by seven species (Davis, 1966). A group of long-haired forms consists of *E. fuscus* (Palisot de Beauvois), *E. andinus* (J. A. Allen), and *E. montosus*

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Thomas. These species are primarily distributed along the Andes of northern South America, and in the lowlands of Colombia and Venezuela, except for *E. montosus*, which occurs from the highlands of Bolivia to the Planalto of southeastern Brazil. A group of short-haired species is represented by *E. innoxius* (Gervais), which occurs along the Pacific Coast in Ecuador and Peru, and by three wide-ranging species from the lowlands east of the Andes (Davis, 1966).

The three eastern species, *E. brasiliensis* (Desmarest), *E. furinalis* (D'Orbigny), and *E. diminutus* Osgood, are apparently sympatric in the Rio Paraná lowlands, along the coast from Maranhão, Brazil, to Buenos Aires, Argentina, and, perhaps, in the vast Caatinga, Serrado, and Chaco regions south of the Amazonian lowlands. The members of this sympatric assemblage are segregated by size, with *E. brasiliensis* being the largest and *E. diminutus* being the smallest. There appears to be some size overlap between species pairs, which has led to considerable confusion concerning the applicable names for certain populations, and the identity of individual bats. Furthermore, there are only a relatively few specimens, from widely scattered localities, of most taxa. Consequently, little is known about individual and secondary sexual variation, and most taxa are poorly characterized.

Early in this study it was discovered that the holotype of *E. dorianus* (Dobson) was much too large to be conspecific with the smallest species of South American *Eptesicus* (*E. dorianus* of Davis, 1966). Other available names for these bats are *E. diminutus* Osgood, 1915, and *E. fidelis* Thomas, 1920. Davis (1966) considered *E. fidelis* as a junior synonym of *E. dorianus*, and regarded *E. diminutus* as conspecific with *E. dorianus*, but recognizable as a subspecies. I also regard *E. diminutus* and *E. fidelis* as being conspecific, and because *E. diminutus* has priority, this name is used to refer to the smallest short-haired South American species of *Eptesicus*.

During the summer of December 1975 and January 1976, I collected and karyotyped specimens of *Eptesicus* from Aguas Chiquitas, a small stream at the southern end of the Sierra de Medina (approximately 800 m), about 4 km E of El Cadillal Dam, Tucumán Province, Argentina. In the process of identifying these specimens, and a specimen from Potrero Dike, El Potrero, Catamarca Province, Argentina, which together span the known size range from *E. diminutus* to *E. brasiliensis*, I have reviewed aspects of the variation and taxonomy of these *Eptesicus* species.

## METHODS

The morphometric traits utilized in this study, their abbreviations, and, where necessary, explanations of the methods of measuring are listed below.

*Cranial breadth* (CB).—Greatest width of cranium immediately posterior to zygomatic arches.

*Length of ear* (EL).

*Length of forearm* (FAL).—Length of forearm, including wrist bones.

*Length of fur* (FL).—Length of pelage in interscapular region.

*Greatest length of skull* (GSL).—Distance from anteriormost point on incisors to posteriormost point of cranium.

*Length of head and body* (HBL).

*Length of hind foot* (HFL).—Length of hind foot, including claws.

*Length of metacarpal 3* (M-III).—Length of metacarpal 3, including wrist.

*Mandibular length* (MNL).—Greatest length of mandible, from front of incisors to back of angular process.

*Length of mandibular toothrow* (MNTL).—Alveolar length of mandibular toothrow, from front of canine to back of M<sub>3</sub>.

*Distance across maxillary toothrows* (MXD).—Greatest distance across upper molar rows, measured from labial sides of molars.

*Length of maxillary toothrow* (MXTR).—Distance from anterior cingulum of canine to back of M<sup>3</sup>.

*Length of phalanx 1 of digit 3* (P1D3).

*Length of phalanx 2 of digit 3* (P2D3).

*Length of tibia* (TBL).

*Length of tragus* (TGL).—Length of tragus, from anterior basal point of origin to tip (measured on dry skins).

*Length of tail* (TL).

*Zygomatic breadth* (ZB).—Greatest distance across zygomatic arches.

Characters, other than standard external measurements and length of fur, were measured with dial calipers and rounded to the nearest 0.1 mm. Length of fur was taken with a millimeter rule, and values were rounded to the nearest millimeter. Measurements of the holotypes of *E. fidelis* and *E. argentinus* Thomas were made by Mr. J. E. Hill. Dr. G. Arbocco took measurements of the holotype of *E. dorianus*. Specimens examined are listed in the discussion section. All specimens are standard skins and skulls and are adult unless otherwise indicated. The acronyms designating the museums of deposition are defined by Choate and Genoways (1975), except for that of the British Museum of Natural History (BMNH).

Samples of males and females of *E. furinalis* from Brazil and from Paraguay were subjected to standard univariate analyses, employing *t*-tests (BMD13D, Dixon, 1976). The sexes of these and other samples of *E. furinalis* and *E. diminutus* were submitted as separate groups in a stepwise discriminant analysis (BMD07M, Dixon 1976). This multivariate analysis tested for sexual dimorphism within populations, and for differences within and between samples. Classification groups were from single localities, except for the Paraguayan samples of *E. furinalis* and for *E. d. diminutus*. The Paraguayan *E. furinalis* come from a relatively small and uniform geographic area (but were initially divided into two samples because of slight color differences). I pooled the two *E. d. diminutus* males to create a classification group for this taxon.

A second stepwise discriminant analysis included samples of *E. brasiliensis*, and additional samples of *E. diminutus* and *E. furinalis*, but utilized only 11 characters. This allowed the incorporation of some samples from Davis (1966) and of specimens with certain missing character values. I pooled the sexes in the samples in order to make all of the data comparable with those of Davis (1966). In this analysis, some obviously misclassified specimens, as determined in the first analysis, were submitted with their appropriate groups. In order to summarize the phenetic relationships among samples, individuals and sample means of short-haired *Eptesicus* from South America were subjected to a hierarchical cluster analysis (MINT), using average Euclidean distance as similarity coefficients. The phenogram was constructed using the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal, 1973). The samples used in this analysis, their origin, and labels are as follows: 1.—*E. b. argentinus* females,

Table 1.—Morphometric traits of *Eptesicus*. Abbreviations are explained in the text.

Species	sex	N	TL	HBL	HF	EL	GSL	CB	ZB	MXTL	MXD
<i>E. brasiliensis</i>											
Catamarca, MSB 32725	♂	1	43	54	8.7	15.8	16.9	8.4	11.8	6.2	6.8
argentinus holotype	♀	1	—	—	—	—	17.3	8.2	12.3	6.3	7.6
melanopterus, CM	♀	1	35	58	8.0	13.0	17.2	8.9	10.5	6.1	7.6
<i>E. diminutus</i>											
<i>fidelis</i> holotype	♂	1	32	50	—	12.5	13.9	7.3	9.8	5.0	5.6
<i>diminutus</i> holotype	♂	1	37	51	10.0	—	14.3	6.6	9.4	5.1	5.8
Maranhão, FMNH 26452	♂	1	33	52	6.5	12.0	14.8	7.4	10.1	5.4	6.3
Minas Geraes, FMNH 20743	♀	1	42	45	7.5	13.2	15.0	7.5	9.6	5.4	6.1
Sao Paulo, MCZ 24821	♂	1	33	52	7.0	13.0	14.3	7.3	9.6	5.0	5.9
Tucumán, CM 42881*	♂	1	32	54	6.2	13.3	13.3	6.5	8.7	4.7	5.5
Tucumán, CM 42880	♀	1	35	54	6.8	13.5	13.8	6.7	9.1	5.0	5.7
Tucumán, CM 42882	♀	1	32	59	7.0	13.6	13.9	7.0	8.9	4.9	5.7
Uruguay, AMNH 205600	♂	1	32	56	6.0	11.0	13.5	6.9	9.0	5.0	6.0
Uruguay, AMNH & FMNH	♀	5	35	52	8.3	12.6	13.9	7.3	9.3	5.0	5.9
Range			33-37	51-53	7.8-9.0	12.0-13.0	13.3-14.7	7.0-7.5	9.1-9.7	4.9-5.1	5.8-6.0
<i>E. dorianus</i> holotype	♀	1	—	—	—	—	17.0	8.5	11.0	6.0	7.5
<i>E. furiinalis</i>											
Brazil, CM	♂	5	39	57	6.6	13.2	16.1	7.9	10.7	5.7	6.6
Range			36-40	52-63	6.0-7.0	12.0-14.0	15.5-16.7	7.8-8.0	10.3-11.0	5.5-5.9	6.3-6.9
Brazil, CM	♀	7	38	59	6.6	14.1	16.1	7.9	10.8	5.8	6.6
Range			33-42	54-68	5.0-7.0	13.0-15.0	16.0-16.5	7.7-8.1	10.3-11.7	5.5-6.0	6.0-6.8
Bolivia, CM 2738	♂	1	40	55	8.0	12.0	15.4	7.4	9.8	5.5	6.2
Paraguay, BMNH 1.8.1.1	♂	1	36	54	—	—	15.2	7.0	9.8	5.3	6.1
Paraguay, UCOON 15649	♀	1	33	53	11.9	13.0	14.7	7.8	10.1	5.4	6.1
Paraguay, UMMZ	♂	7	39	54	9.3	14.6	15.5	7.7	10.4	5.6	6.4
Range			36-41	51-56	8.0-9.9	13.0-15.0	14.9-16.1	7.3-8.1	10.2-10.9	5.3-5.7	6.2-6.6
Paraguay, UCONN & UMMZ	♀	12	36	55	8.8	13.7	15.7	7.8	10.5	5.6	6.4
Range			35-40	52-63	8.0-9.9	12.0-15.0	15.0-16.8	7.4-8.3	9.9-11.7	5.4-6.0	6.2-6.6
Tucumán, CM 42883	♂	1	40	62	7.7	15.0	15.5	7.0	10.4	5.7	6.6
Tucumán, CM 42884	♀	1	41	70	8.9	15.2	16.9	7.7	11.3	6.0	6.8
Tucumán, CM 42885	♀	1	45	69	10.1	15.0	16.4	7.5	11.4	6.1	7.1
Tucumán, CM 42886*	♀	1	37	65	8.3	14.7	14.0	7.5	11.0	5.8	6.6



Table 1.—(Continued)

Species	sex	N	MNL	MNTL	FAL	M-III	P1D3	P2D3	FL	TBL	TGL
<i>E. brasiliensis</i>											
Catamarca, MSB 32725	♂	1	12.6	6.7	41.3	40.4	14.0	11.5	6	14.6	5.1
argentinus holotype	♀	1	12.9	7.2	45.5	42.0	15.0	12.0	—	—	—
melanopterus, CM	♀	1	12.7	6.4	39.3	36.5	12.9	11.8	5	—	4.7
<i>E. diminutus</i>											
fidelis holotype	♂	1	10.0	5.3	34.0	29.0	11.0	9.5	—	—	4.2
diminutus holotype	♂	1	10.0	5.6	35.7	33.0	12.6	9.8	—	14.3	4.5
Maranhão, FMNH 26452	♂	1	10.6	5.8	37.9	35.2	12.8	10.9	6	14.7	4.9
Minas Geraes, FMNH 20743	♂	1	—	5.8	36.0	33.5	13.1	10.6	5	14.2	5.0
Sao Paulo, MCZ 24821	♂	1	10.4	5.6	34.1	30.8	11.1	9.6	5	12.9	4.5
Tucumán, CM 42881*	♂	1	9.5	5.0	32.1	30.1	10.3	9.0	5	11.8	4.0
Tucumán, CM 42880	♀	1	10.0	5.2	32.6	31.5	10.4	9.4	5	12.5	4.5
Tucumán, CM 42882	♀	1	10.2	5.2	33.6	31.3	11.2	9.3	5	12.7	4.2
Uruguay, AMNH 205600	♂	1	10.2	5.2	31.5	30.5	10.7	9.1	5	—	—
Uruguay, AMNH & FMNH	♀	5	10.3	5.3	32.4	30.2	10.8	8.9	6	11.7	4.2
Range			10.2–10.5	5.2–5.5	31.5–32.4	28.5–30.8	10.4–11.5	8.6–9.6	5–6	11.5–11.8	4.0–4.5
<i>E. dorianus</i> holotype	♀	1	12.6	6.8	41.0	38.5	14.5	13.0	—	—	—
<i>E. furinatis</i>											
Brazil, CM	♂	5	12.0	5.9	39.0	37.8	13.8	11.4	6	14.2	4.7
Range			11.6–12.3	5.7–6.2	37.5–41.1	35.9–39.5	13.4–14.6	10.6–12.3	5–6	13.1–15.0	4.8–5.1
Brazil, CM	♀	7	12.4	6.0	40.0	38.2	14.7	11.9	6	15.0	4.9
Range			12.0–12.7	5.8–6.1	38.9–41.9	37.3–39.3	14.4–15.5	11.0–12.9	4–6	14.4–15.9	4.7–5.2
Bolivia, CM 2738	♂	1	11.8	5.7	38.2	35.6	13.8	11.8	6	14.3	4.0
Paraguay, BMNH 1.8.1.1	♂	1	11.3	5.8	36.3	34.5	12.0	9.5	—	—	—
Paraguay, UCONN 15649	♀	1	11.3	5.7	34.8	34.2	12.1	9.9	7	—	4.4
Paraguay, UMMZ	♂	7	11.5	5.9	37.4	35.7	13.1	10.9	6	14.9	4.9
Range			10.9–11.8	5.5–6.7	35.8–39.3	34.4–36.9	11.9–14.2	10.0–11.9	5–7	14.1–16.1	4.5–5.1
Paraguay, UCONN & UMMZ	♀	12	11.7	6.0	37.4	36.2	13.3	11.0	6	14.0	4.6
Range			11.0–12.4	5.7–6.4	34.3–39.8	32.9–38.9	12.1–15.1	10.3–12.3	5–7	12.1–15.1	4.3–5.2
Tucumán, CM 42883	♂	1	11.9	6.2	39.3	38.1	14.0	12.5	6	14.9	5.0
Tucumán, CM 42884	♀	1	12.6	6.5	41.1	39.5	15.1	12.9	7	15.8	5.3
Tucumán, CM 42885	♀	1	12.8	6.7	39.8	38.1	15.4	12.3	7	16.0	5.2
Tucumán, CM 42886*	♀	1	11.9	6.4	39.7	33.6	13.0	10.3	7	14.5	4.5

\* Juvenile.

mean values of three specimens from Davis (1966); 2.—*E. b. argentinus* male from Catamarca, MSB 32725; 3.—*E. b. brasiliensis* males, mean values of two specimens from Davis (1966); 4.—*E. b. melanopterus*, mean values of 20 specimens from Davis (1966); 5.—*E. b. melanopterus* male from Surinam, CM (uncatalogued); 6.—*E. b. thomasi*, mean values of 20 specimens from Davis (1966); 7.—*E. b. thomasi* holotype; 8.—*E. b. argentinus* holotype; 9.—*E. dorianus* holotype; 10.—*E. innoxius* males, mean values of four specimens from Davis (1966); 11.—*E. innoxius* females, mean values of 13 specimens from Davis (1966); 12.—*E. diminutus* holotype; 13.—*E. diminutus* male from Maranhão, FMNH 26492; 14.—*E. diminutus* female from Minas Geraes, FMNH 20743; 15.—*E. diminutus* male from São Paulo, MCZ 24821; 16.—*E. d. fidelis* holotype; 17.—*E. d. fidelis* male from Uruguay, AMNH 20960; 18.—*E. d. fidelis* females from Uruguay, mean values of five specimens, AMNH and FMNH; 19.—*E. d. fidelis* females from Tucumán, mean values of two specimens, CM; 20.—*E. f. furinalis* male from Paraguay, BMNH 1.8.1.1; 21.—*E. f. gaumeri* holotype; 22.—*E. f. gaumeri*, mean values of nine specimens from Davis (1966); 23.—*E. f. chapmani* holotype; 24.—*E. f. chapmani*, mean values of 21 specimens from Davis (1966); 25.—*E. f. furinalis* female from Jujuy, AMNH 180305; 26.—*E. f. furinalis*, mean values of 33 specimens from Davis (1966); 27.—*E. furinalis* male from Tucumán, CM 42883; 28.—*E. furinalis* females from Tucumán, mean values of two, CM; 29.—*E. f. chapmani* male from Bolivia, CM 2738; 30.—*E. f. chapmani* males from Brazil, mean values of five, CM; 31.—*E. f. chapmani* females from Brazil, mean values of seven, CM; 32.—*E. f. furinalis* males from Paraguay, mean values of five, UMMZ; 33.—*E. f. furinalis* females from Paraguay, mean values of 12, UCONN and UMMZ.

Chromosome preparations of humeral marrow cells were made using the *in vivo* colchicine, hypotonic sodium-citrate technique. Procedures and nomenclature follow Patton (1967).

## RESULTS

Females averaged larger than males in most characters (Table 1), although few of the differences were significant. Females of *E. furinalis* from Crato, Ceara, Brazil, were significantly larger than males in mandibular length ( $P = 0.03$ ) and length of phalanx 1 of digit 3 ( $P = 0.03$ ). There were no significant differences between the Paraguayan samples of *E. furinalis*. Females and males were readily distinguishable by the discriminant function analysis, and there was no misclassification of the sexes in the samples of *E. furinalis*. Table 2 presents the results of discriminant analysis I, based upon 16 morphometric traits. Note that males and females of the Brazilian and Paraguayan populations are most similar to each other. Thus, although the sexes are distinctive, the populations form discreet morphological units. Table 3 lists the characters used in this analysis and orders them from the most to the least useful for distinguishing groups.

Canonical analysis provides a mechanism of graphically portraying the phenetic relationships among these samples (Fig. 1). The first two canonical variates account for 71.2% of the total dispersion (Variate I = 44.9%). Note in Fig. 1 that the sexes are readily separable except for one female of *E. furinalis*, which is plotted among the males. This specimen is, however, closest to the other females. The Brazilian samples of *E. furinalis* are distinct from those from Paraguay, and the

Table 2.—Mean squared Mahalanobius distance values ( $D^2$ ) of *Eptesicus* samples, based upon the linear discriminant function of Analysis I.

	Samples												
	2	5	7	8	9	10	11	13					
<i>diminutus</i>													
1. <i>fidelis</i> holotype	56.0	103.7	167.1	205.7	112.7	146.7	135.5	266.8					
2. <i>diminutus</i> males	9.7	97.0	114.5	135.9	60.8	86.3	80.8	177.2					
3. <i>diminutus</i> female	154.4	190.3	153.0	163.4	142.7	214.8	186.5	212.0					
4. São Paulo male	50.5	46.7	78.8	112.7	61.6	90.8	83.8	153.1					
5. Tucumán females	91.9	4.1	99.4	135.9	116.5	126.9	161.4	176.2					
<i>furinalis</i>													
6. UCONN 15649, female	101.1	111.5	71.9	104.2	40.0	30.7	46.4	192.8					
7. Brazil males	118.0	108.8	13.5	26.0	55.0	48.5	69.8	76.4					
8. Brazil females	140.4	145.5	26.5	13.7	68.6	69.7	96.1	58.4					
9. Paraguay, UMMZ males	64.1	125.5	54.4	67.7	13.0	28.7	44.1	109.3					
10. Paraguay, UMMZ females	89.7	133.8	48.1	69.1	28.8	13.1	38.0	118.6					
11. Paraguay, UCONN females	86.6	172.8	71.8	97.9	46.6	41.4	15.5	162.6					
12. Tucumán male	153.5	137.8	71.5	60.1	24.7	130.9	156.1	36.2					
13. Tucumán females	173.8	178.3	69.1	58.9	102.5	111.7	153.2	6.2					

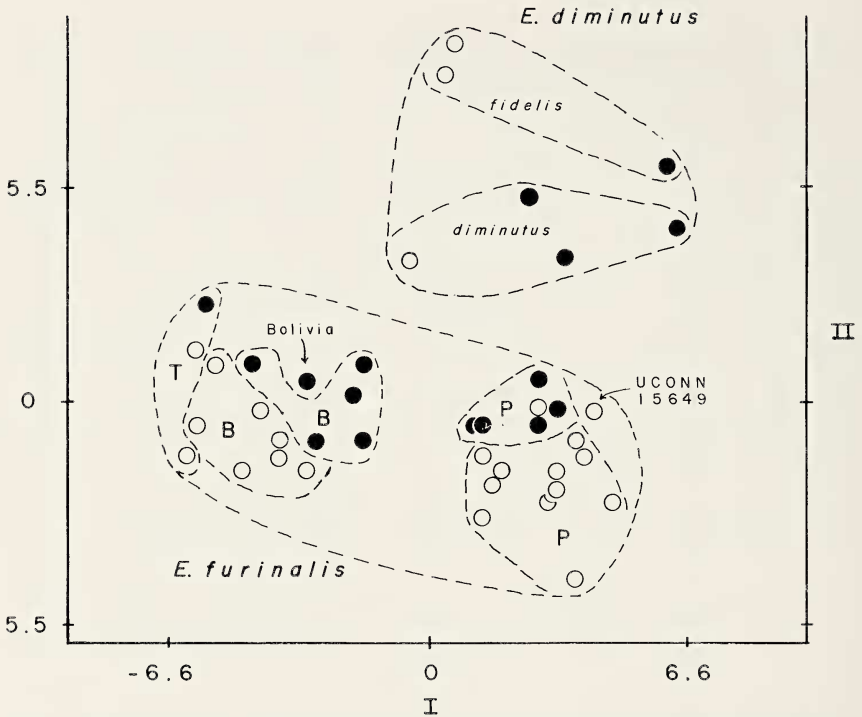


Fig. 1.—Bivariate plot of canonical variates I and II for samples of *E. diminutus* and *E. furinalis*. Open circles = females; closed circles = males; B = Brazil; P = Paraguay; T = Tucumán.

specimens of *E. furinalis* from Tucumán Province, Argentina, and from Bolivia are phenetically most similar to the Brazilian samples (Fig. 1 and Table 2). The Paraguayan specimen of *E. cf. fidelis* (UCONN 15649) of Wetzel and Lovett (1974), is assigned to *E. furinalis* (Table 2 and Fig. 1).

The variables with the highest positive canonical coefficients for Variate I (arbitrarily, those with values greater than 1.0), include, in order of decreasing values, cranial breadth, length of maxillary tooth-row, zygomatic breadth, and length of hind foot. The larger negative coefficients, in descending order, are mandibular length, distance across the molar rows, and greatest length of skull. Size has relatively little influence on Variate I. The only character with a positive coefficient for Variate II, greater than 1.0, was length of maxillary tooth-row. Negative coefficients with values less than  $-1.0$  are distance across the molar rows, mandibular length, zygomatic breadth, length of phalanx 1 of digit 3, and length of hind foot. The smallest bats were



Table 3.—Variables used in the discriminant function analyses, listed in order of their usefulness in distinguishing groups. The character with the greatest between groups variance and the least within groups variance is selected first. Other traits are ranked using the same criteria. The statistics are recalculated at each step.

Step	Discriminant Analysis I			Discriminant Analysis II		
	Trait	F-value	U-statistic	Trait	F-value	U-statistic
1.	MNL	25.14	0.1373	MXTL	38.85	0.1207
2.	HFL	11.91	0.0336	MNL	7.99	0.0477
3.	CB	4.16	0.0158	MNTR	4.62	0.0251
4.	HBL	4.21	0.0073	P1D3	3.61	0.0146
5.	MNTL	2.39	0.0043	CB	2.77	0.0093
6.	TBL	2.38	0.0025	MXD	2.82	0.0058
7.	P1D3	1.86	0.0016	FAL	2.59	0.0038
8.	TL	2.26	0.0009	P2D3	2.06	0.0026
9.	ZB	3.07	0.0004	M-III	1.68	0.0019
10.	FAL	1.25	0.0003	ZB	1.47	0.0014
11.	MXTL	0.87	0.0002	GSL	0.45	0.0013
12.	MXD	0.78	0.0002			
13.	TGL	0.74	0.0001			
14.	M-III	0.78	0.0001			
15.	P2D3	0.69	0.0000			
16.	GSL	0.79	0.0000			

positioned at the positive end, and larger animals at the negative end of Variate II.

The results of the second discriminant function/canonical analysis are presented in Table 4 and Fig. 2. In this analysis the sexes were pooled, the character suite was reduced to 11, and additional samples, including *E. brasiliensis*, were added. The sexes are generally identifiable within samples, and overlap between taxa typically involves males of the larger OTU and females of the smaller OTU (Fig. 2). The variables utilized in this analysis are presented in Table 3. Variables with the highest positive coefficients for Variate I (those with values greater than 1.0) are distance across the molar rows and length of mandibular tooththrow. High negative coefficients were not scored for Variate I. For Variate II, length of mandibular tooththrow and length of maxillary tooththrow had high positive coefficients, and mandibular length had a high negative coefficient. Canonical Variate I appears to be strongly influenced by size, with small bats positioned on the negative pole and large bats on the positive pole.

The holotype of *E. dorianus* falls within the distribution of *E. brasiliensis argentinus* for Canonical Variates I and II (Fig. 2), and is closest, overall, to *E. brasiliensis melanopterus* (Jentink) in terms of its position on the linear discriminant functions (Table 4). The specimen from Villa Rica, Depto. Villarrica, Paraguay (BMNH No. 1.8.1.1, *E.*

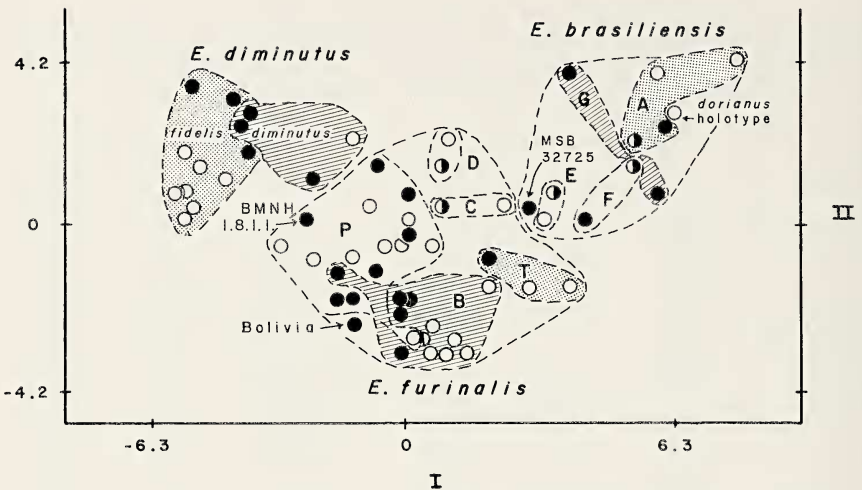


Fig. 2.—Bivariate plot of canonical variates I and II for samples of *E. brasiliensis*, *E. diminutus*, and *E. furinalis*. Open circles = females; closed circles = males; half open circles = sex unknown or samples of mixed sexes; A = *E. b. argentinus*; B = *E. f. chapmani* from Brazil; C = *E. f. chapmani* from Davis (1966); D = *E. f. furinalis* from Davis (1966); E = *E. b. melanopterus*; F = *E. b. thomasi* from Davis (1966); G = *E. b. brasiliensis* from Davis (1966); P = *E. f. furinalis* from Paraguay; T = *E. furinalis* from Tucumán. See text for further explanation.

*dorianus* of Davis, 1966), is placed within the sample of Paraguayan *E. furinalis* (Table 4 and Fig. 2). Measurements from Davis (1966) of *E. f. furinalis* are somewhat intermediate to the samples of *E. furinalis chapmani* Allen and to samples of *E. furinalis* from Paraguay and from Tucumán, Argentina. This is not surprising, as the one specimen (AMNH 180305) is from northwestern Argentina (Jujuy Province), near the range of *E. f. chapmani*, and the sample means included specimens from northwestern Argentina and from several localities in Paraguay (Davis, 1966). There is a near continuum of variation in these samples (Fig. 2). If, however, one looks at potentially sympatric populations, there is a clearer separation of taxa. In Fig. 2, the stippled areas indicate the positions of three sympatric populations in northwestern Argentina, and the lined areas signify the three potentially sympatric populations in Brazil. The separation of *E. f. chapmani* and

→  
Fig. 3.—Phenogram of South American short-haired *Eptesicus* species, computed from average Euclidean distance values and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The numbers designating taxa and localities are defined in the text. The cophenetic correlation coefficient for the phenogram is 0.737.

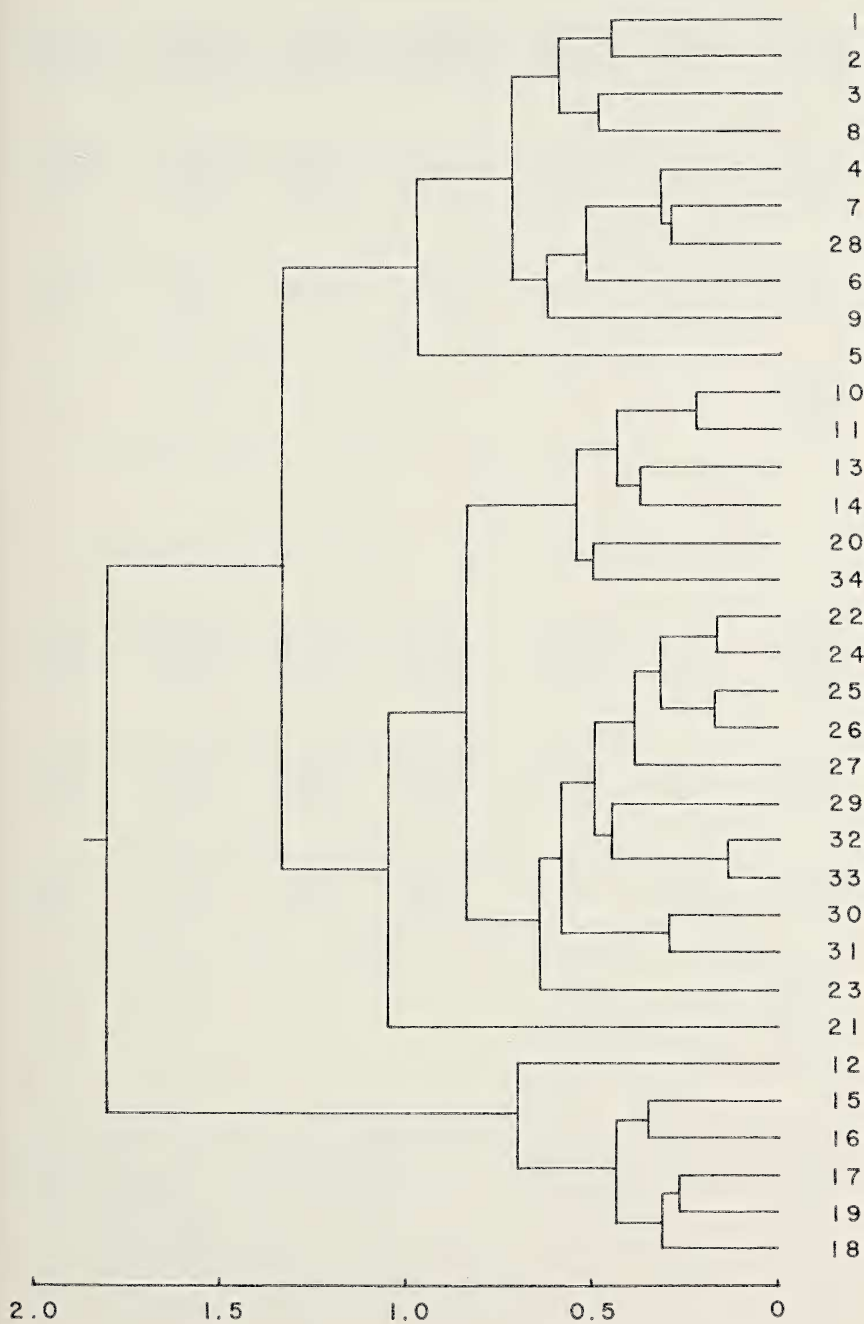


Table 4.—Mean squared Mahalanobis distance values ( $D^2$ ) of *Eptesicus* samples, based upon the linear discriminant function of Analysis II.

Samples	Samples													
	1	2	3	4	7	8	9	11	13	14				
<i>brasiliensis</i>														
1. <i>argentinus</i>	8.9	26.9	42.7	39.0	151.9	171.6	106.9	83.4	81.3	56.7				
2. <i>brasiliensis</i>	23.6	5.6	37.8	35.2	123.3	135.7	74.2	59.5	58.7	47.9				
3. <i>melanopterus</i>	45.6	43.9	11.7	26.2	94.6	112.3	75.0	41.8	44.3	35.2				
4. <i>thomasi</i>	36.4	35.9	20.7	6.3	119.9	129.6	89.6	53.0	60.7	28.6				
5. Catamarca, MSB 32725	32.2	24.3	40.1	53.1	87.0	98.4	56.6	33.7	27.1	41.8				
<i>doritanus</i>														
6. holotype	124.8	147.9	118.5	143.7	252.3	298.5	232.0	200.0	185.3	129.7				
<i>diminutus</i>														
7. <i>fidelis</i> , Uruguay*	152.3	127.1	92.2	122.9	9.3	16.8	24.8	58.0	34.3	91.5				
8. <i>fidelis</i> , Tucumán	165.3	132.6	103.1	125.8	10.1	2.6	20.0	55.6	34.6	94.0				
9. <i>diminutus</i>	105.4	76.0	70.6	90.7	22.8	24.8	7.3	41.8	23.3	65.3				
<i>furinalis</i>														
10. BMNH 1.8.1.1	109.8	92.6	65.9	84.1	20.6	23.1	27.6	29.3	18.3	46.9				
11. Brazil	84.2	63.6	39.8	56.5	58.4	62.8	44.2	9.5	16.8	30.0				
12. Bolivia	119.1	84.6	50.0	61.8	39.2	38.6	36.7	14.2	20.3	34.6				
13. Paraguay	82.7	63.3	42.8	64.6	35.2	42.3	26.2	9.5	37.4	35.2				
14. Tucumán	54.2	48.6	29.9	28.7	88.5	97.8	64.3	26.7	33.6	64.0				
15. Yuto, Jujuy	47.3	32.6	29.7	30.1	43.5	49.6	22.5	32.1	21.3	20.5				
16. <i>furinalis</i> , mean	51.5	32.4	28.8	31.9	42.6	45.0	17.8	22.8	15.4	17.5				
17. <i>chapmani</i> , holotype	58.1	43.1	26.6	24.1	79.4	80.7	47.9	37.1	35.3	20.6				
18. <i>chapmani</i> , mean	56.3	36.6	21.2	28.0	44.7	50.4	22.6	18.0	13.8	12.7				

\* Includes the holotype of *fidelis*.



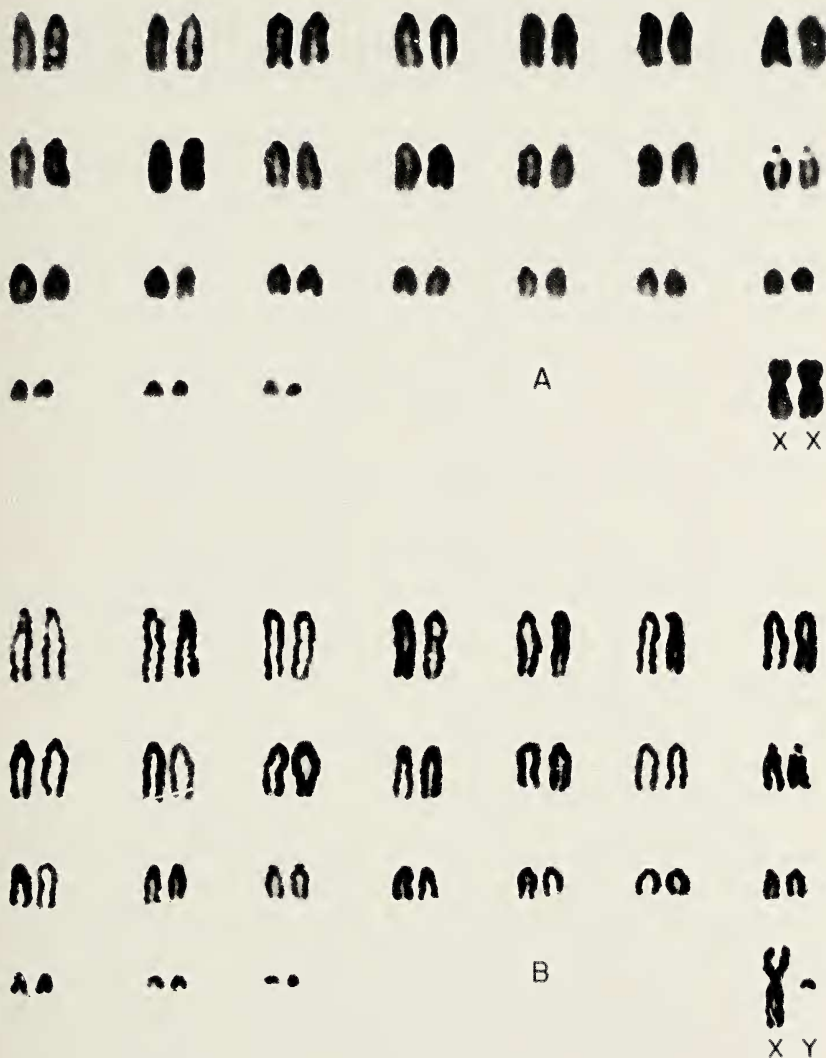


Fig. 4.—Karyotypes of *Eptesicus*. A, *E. furinalis* female from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina, CM 42886; B, *E. diminutus* male from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina, CM 42881.

*E. b. melanopterus* from Amazonia is less satisfactory (Fig. 2 and Table 4), and the relationships of these taxa to those of other populations of *E. brasiliensis* and *E. furinalis* are poorly resolved by this analysis.

The results of the hierarchical cluster analysis (UPGMA) are presented in Fig. 3. Note in the phenogram that there are three main clusters, representing, from top to bottom, big bats (primarily *E. brasiliensis*), intermediate-sized bats (*E. innoxius*, *E. furinalis*, and two *E. diminutus*), and small bats (*E. diminutus*). The intermediate-sized bat cluster is divisible into two distinct units—an *E. furinalis* cluster and a cluster of relatively small bats, including *E. innoxius*, two small *E. furinalis*, and two large *E. diminutus* specimens. These two *E. furinalis* specimens are the two to the far left in the *E. furinalis* cluster of Fig. 2. The two *E. diminutus* specimens are the two on the extreme right in the *E. d. diminutus* cluster of Fig. 2. The male of *E. furinalis* from Tucumán is closely linked with *E. furinalis* specimens from northwestern Argentina in this UPGMA analysis (Fig. 3), but the females are linked with *E. b. thomasi* and *E. b. melanopterus*. This reflects the relatively large size of this sample of *E. furinalis* females.

The 50 chromosomes of *E. furinalis* and *E. diminutus* are identical in gross morphology, and consist of 48 acrocentric autosomes ( $2N = 50$ ,  $FN = 48$ ), with a large submetacentric X and a small acrocentric Y. One pair of intermediate-sized autosomes has a subcentromeric secondary construction (Fig. 4).

#### DISCUSSION

The karyotypes of *E. furinalis* and *E. diminutus* appear identical in gross morphology to the North American forms, *E. furinalis gaumeri* J. A. Allen, *E. andinus*, and *E. fuscus* (Baker and Patton, 1967), to the Caribbean species, *E. guadeloupensis* Genoways and Baker (1975), and to the Old World species, *E. serotinus* (Schreber) (Baker et al., 1974; Fedyk and Fedyk, 1970) and *E. hottentotus* (A. Smith) (Peterson and Nagorsen, 1975). This eptesicoid karyotype is also identical in appearance to that of the South American big-eared bat, *Histiotus montanus* (Philippi and Landbeck) (Williams and Mares, 1978). The only variation in this eptesicoid karyotype noted to date is in the morphology of the Y chromosome of *E. serotinus* from Poland, which have a submetacentric Y rather than the typical acrocentric Y (Fedyk and Fedyk, 1970). It is of particular note that the small South American species, *E. furinalis* and *E. diminutus*, exhibit the eptesicoid karyotype, whereas the small African species, *E. capensis* (A. Smith), has a karyotype consisting of a  $2N$  of 32 and an  $FN$  of 50 (Peterson and Nagorsen, 1975). This latter karyotype appears most similar to those of several species of *Pipistrellus* (Capanna and Civitelli, 1970).

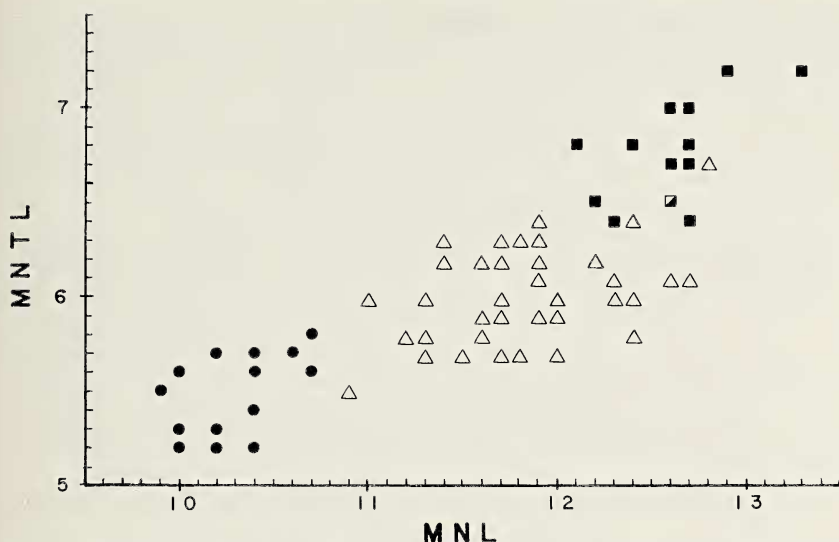


Fig. 5.—Bivariate plot of mandible length (MNL) and mandibular tooththrow length (MNTL) for individuals of *Eptesicus*. Circles = *E. diminutus*; triangles = *E. furinalis*; squares = *E. brasiliensis*.

Sexual size dimorphism in *E. furinalis* and *E. diminutus* is apparent. As is the typical pattern in vespertilionid bats (Williams and Findley, 1979), females average larger than males. These size differences have apparently been a major reason for species misidentification. Small males of *E. furinalis* can be confused with the larger females of *E. diminutus*. *E. brasiliensis* is probably also size dimorphic, although the samples utilized in this study were not all identifiable by sex. Misidentification between *E. furinalis* and *E. brasiliensis* would most likely involve large *E. furinalis* females and small *E. brasiliensis* males.

The overlap in size in these three species makes it difficult to characterize the species. This size continuum is well illustrated by plotting mandibular length against length of mandibular tooththrow (Fig. 5). These are two of the best characters for distinguishing species (see Table 3), but they cannot distinguish all specimens. Other than a complex linear discriminant function (which separates most populations of these species), there is no single characteristic, among the ones studied, that will distinguish all *E. diminutus*, *E. furinalis*, and *E. brasiliensis*. There should be relatively good size differences, however, between these short-haired species in any single area. In identifying specimens, it is essential that they are properly sexed. When measuring mandibular length, one must be certain that the angular process of the mandible is intact. Length of forearm of adult specimens should

prove sufficiently reliable to identify most specimens in the field (see Table 1 and Davis, 1966).

### *Eptesicus brasiliensis*

There may be some question as to the identity of the specimen from Potrero Dike, El Potrero, Catamarca Province, Argentina (MSB 32725), designated as *E. brasiliensis* (see Tables 1 and 4, and Fig. 3). It is structurally most similar to the *brasiliensis* complex, but is somewhat smaller than other *E. brasiliensis*. As the other included individuals of *E. b. argentinus* are females or of unknown sex, its smaller size may simply reflect one extreme of normal variation. It does appear to be quite similar in dimensions to a specimen from nearby Mendoza (Massoia, 1976), which I consider to be *E. brasiliensis*. The long, subacute tragus of MSB 32725 is unlike any *Eptesicus* I have seen, but I do not know if this tragus shape is characteristic for some populations of *E. brasiliensis*.

The samples of *E. brasiliensis melanopterus* consist of a male from Keizerstraat, Paramaribo, Surinam (CM), the type locality for *E. melanopterus* (Jentink), and the means of a sample reported by Davis (1966). This latter sample was identified as *E. furinalis* by the discriminant function analysis, and was linked with a cluster consisting of the *E. b. thomasi* Davis holotype and the females of the Tucumán sample of *E. furinalis* in the UPGMA analysis (Fig. 3). It is possible that this sample contains individuals of both *E. furinalis* and *E. b. melanopterus*. The topotype of *E. b. melanopterus* is the most distinctive of the *E. brasiliensis* cluster in the UPGMA analysis. It has a greatly inflated braincase and a large sagittal crest. The crest is unusual for a bat the size of *E. b. melanopterus* (which is similar in size to *E. furinalis*). The specific status of *E. b. melanopterus* and the systematic relationships of *Eptesicus* populations from Amazonia and the northern South American lowlands are, in my opinion, still unresolved.

### *Eptesicus furinalis*

The outlines of the phenetic relationships of the South American populations of *E. furinalis* (*E. f. gaumeri* excluded) are clear, although many details must still be worked out as adequate material becomes available. Individuals from the Rio Paraná/Rio Uruguay and Chaco Boreal lowlands are small for *E. furinalis* (Table 1) and are nearly black in color (in fresh pelage), although in the western Chaco of Paraguay they are browner. The name *E. f. furinalis* (D'Orbigny) applies to this population. Intermediate-sized bats from Amazonia, and from the lower Andean slopes in Bolivia form a second morphologic unit, *E. f. chapmani*. Specimens from the Caatinga region of Brazil seem most closely related to *E. f. chapmani* (Figs. 2 and 3). Bats from the



higher, mixed mesic Chaco region of Tucumán, Salta, and Jujuy provinces, Argentina, are large, and are brownish chestnut or auburn in color. They are more similar to *E. f. chapmani* than to the geographically adjacent *E. f. furinalis* (Tables 1, 2, and 4; Figs. 1–3). This population is distinctive, and is hereby named.

### ***Eptesicus furinalis findleyi*, new subspecies**

*Holotype*.—Adult female; skin, skull, and chromosomes, CM 42884; from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina; obtained 29 December 1975 by D. F. Williams, original no. 2044.

*Distribution*.—Known from along the eastern Andean foothills, from Tucumán, northward in Jujuy and Salta provinces, Argentina.

*Diagnosis*.—A large, chestnut or auburn brown member of the *E. furinalis* complex. Hairs on underparts light buffy-tipped. Membranes, ears, and lips dark brownish-black. Fur intermediate in length.

*Etymology*.—This population is respectfully named for James S. Findley, in honor of his many contributions to chiropteran biology.

*Description*.—Size intermediate for *Eptesicus* and large for *E. furinalis* (see Table 1). Color above between Chestnut and Auburn (Ridgway, 1912), with a glossy sheen; hairs blackish basally. Underparts with light buffy-tipped hairs (closest to Warm Buff, Ridgway, 1912); hairs blackish basally except for the posterior pelvic region, where they are buffy throughout their length. Dorsal pelage of intermediate length, averaging about 7 mm. Membranes, lips, and ears dark brownish-black; membranes naked. Tragus relatively long, with a rounded and anteriorly inflected tip. Skull with weakly developed sagittal crest (Fig. 6). Karyotype of typical eptesicoid pattern, with a 2N of 50, and 48 autosomal arms; autosomes all acrocentric; one pair of intermediate-sized autosomes with a subcentromeric heterochromatic band; X chromosome large and submetacentric; Y chromosome small and acrocentric (Fig. 4).

*Comparisons*.—*Eptesicus furinalis findleyi* is larger than *E. f. furinalis* (see Table 1), is brownish-chestnut or auburn rather than brownish-black, has a glossy sheen to the fur, and has a relatively longer tragus and smaller hind foot. From *E. f. chapmani*, *E. f. findleyi* can be distinguished by its richer chestnut or auburn brown color with a glossier sheen, its buffy rather than grayish underparts, and by its larger size (Table 1).

*Remarks*.—Specimens from Jujuy and Salta provinces are somewhat intermediate (that is, they are smaller and darker than *E. f. findleyi* from Tucumán) to both *E. f. chapmani* and *E. f. furinalis*. This is especially true of specimens from Yuto, Jujuy.

*Specimens examined*.—ARGENTINA. *Jujuy*: Ledesma, 1♂ (AMNH); Santa Barbara, 1♂, 1♀ (AMNH); Yuto, 11♂, 8♀ (AMNH). *Salta*: 24 km NW Agua Blanca, Departamento Orán, 1♂ (MSB). *Tucumán*: Aguas Chiquitas, about 800 m, Sierra de Medina, 1♂, 3♀ (1 juvenile) + chromosomes (CM).

*Referred material*.—ARGENTINA. *Jujuy*: Palma Sola, 550 m (Villa-R. and Cornejo,

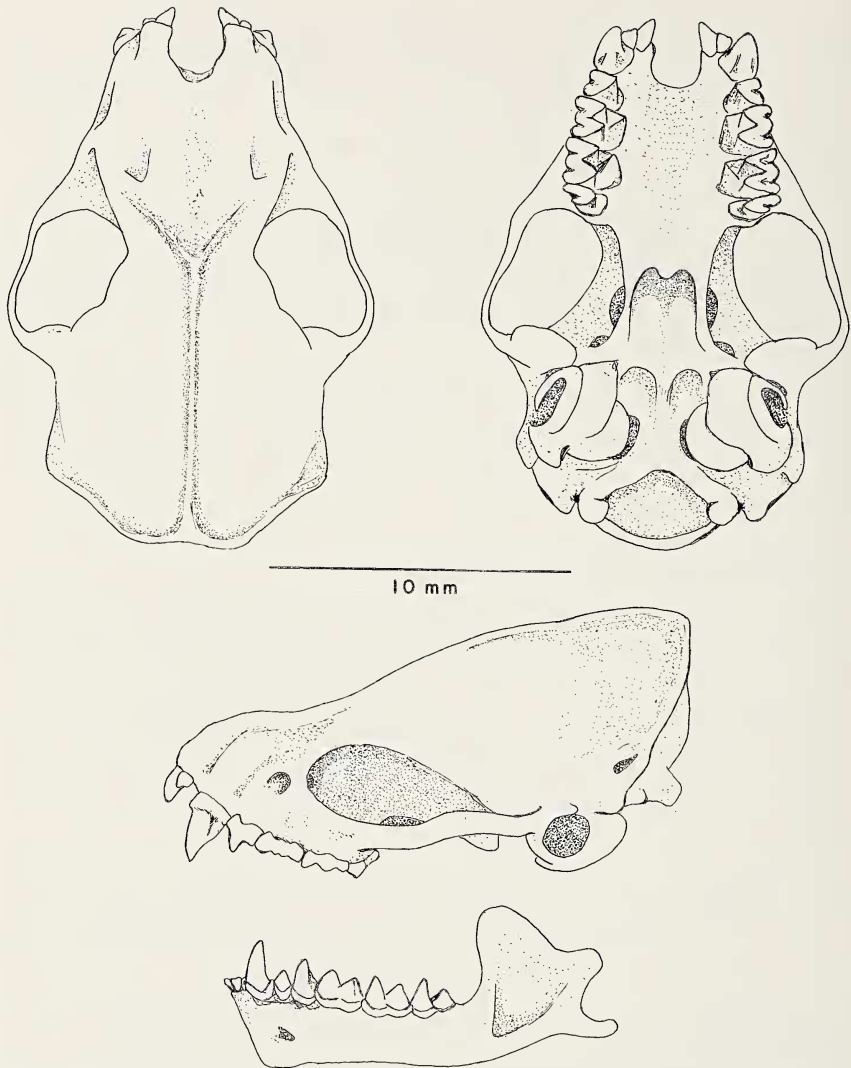


Fig. 6.—Skull of *Eptesicus furinalis findleyi*. A camera lucida drawing, based upon the holotype (CM 42884).

1969). *Tucumán*: Concepcion, 1♀ (BMNH); Tucumán, 450 m, 1♂ (BMNH) (Davis, 1966).

Comparative material of *E. furinalis*, examined and referable to other subspecies are listed below:

*E. furinalis furinalis*.—PARAGUAY. *Boquerón*: line camp, Juan de Zalazar, 1♀ (UCONN); 0.75 km N line camp, Juan de Zalazar, 1♀ (UCONN); 3 km SE line camp,



Fig. 7.—Distribution of *Eptesicus diminutus*. Type localities are designated by two concentric circles. Open circles = *E. d. diminutus*; solid circles = *E. d. fidelis*.

Rio Verde, Juan de Zalazar, 1♀ (alc.) (UCONN); 4 km N Rio Verde, Juan de Zalazar, 1♀ (UCONN). *Caaguazú*: Sapucay, 4♂, 7♀ (AMNH). *Central*: Asunción, 1♀ (UMMZ); Asunción, Recoleta, 5♂, 4♀ (1 skull only) (UMMZ); San Lorenzo, 1♀ (UCONN). *Cordillera*: Tobati, 1♂ (UCONN). *Czsendeyó*: 6.3 km NE Curuzuábá, 1♂ (UMMZ). *Guaira*: Itapé, 2♂ (AMNH). *Itapúa*: 1 km N Rio Paraná, left bank Rio Pirapó, 2♂ (alc.) (UCONN). *Neuva Asunción*: 49.6 km N (by Rd.) Filadelfia, 1♂ (UMMZ).

*E. furinalis chapmani*.—BRAZIL. *Amazonas*: Rio Negro, Igarapé Cação Pereira, near Manaus, 3♂, 1♀ (AMNH); Rio Madeira, Rasarinho, Lago Miguel, 1♂ (AMNH). *Ceara*: Foresta Nacional de Araripe, Crato, 6♂ (1 juvenile), 8♀ (1 juvenile) (CM—uncataloged). BOLIVIA. *Santa Cruz*: Provincia del Sara, 1♂ (CM).

### *Eptesicus diminutus*

The smallest South American *Eptesicus*, *E. diminutus*, is found in the Rio Paraná/Rio Uruguay lowlands, in the mixed mesic Chaco region of Tucumán, Argentina, and the eastern Brazilian highlands from Maranhão to São Paulo (Fig. 7). The lowland population was named *E. fidelis* by Thomas (1920), who considered *E. dorianus* to be a synonym of *E. furinalis* on the basis of Dobson's (1885) measurements. Subsequently, *E. fidelis* was synonymized with *E. dorianus* by Davis (1966), who concluded that those measurements placed *E. dorianus* within the size range of the smallest *Eptesicus*. Davis' (1966) characterization of this species was based upon a series of specimens that included a male *E. furinalis* (BMNH 1.8.1.1) as well as upon Dobson's (1885) measurements of the holotype of *E. dorianus*. Measurements of the holotype of *E. dorianus* (Table 1), provided by Dr. Arbocco, show this specimen to be too large to be either *E. diminutus* or *E. furinalis*. The multivariate analyses (Table 4 and Figs. 2 and 3) place this specimen with *E. brasiliensis*, but it is not an especially close association. As the measurements of the holotype do not correspond to those of Dobson (1885), a mixup is evident. Measurements of the holotype, followed by Dobson's (1885) measurements of the same specimen (converted from inches and tenths to millimeters) are as follows: length of forearm, 41 (36.8); length of metacarpal 3, 38.5 (33.0); length of phalanx 1 of digit 3, 14.5 (11.4). Obviously, the specimen now designated as the holotype may not be the one upon which Dobson based his description of *E. dorianus*. An alternate explanation, however, is that Dobson somehow erred in recording or transcribing the measurements. That this is a possibility is suggested by the fact that he explicitly compares *E. dorianus* with *E. hilarii* (Geoffroy), stating "about the size of *V. hilarii* which it closely resembles in the form of the ears and teeth but differs from in its shorter tail and ears (the forearm being the same length in both species)" (Dobson, 1885). The name *E. hilarii* was generally applied to populations of *E. brasiliensis* at the time Dobson described *E. dorianus*.

I believe that, on the basis of Dobson's measurements, *E. dorianus* (Dobson, 1885) is a junior synonym of *E. furinalis* (D'Orbigny, 1847).



However, if the specimen presently designated as the holotype can be shown to be the one that Dobson described, then the name *E. dorianus* may apply to the population now known as *E. brasiliensis argentinus* Thomas, 1920. Alternately, the holotype may be an Old World *Eptesicus*, a mixup in specimens occurring either prior to, or after Dobson described *E. dorianus*. Perhaps the best way to treat the name *E. dorianus* (Dobson), and the one I prefer, is to designate it as a *nomen dubium*, as it cannot be applied with certainty to any known taxon.

*E. diminutus fidelis* from the lowlands of the Rio Paraná and Rio Uruguay are slightly larger and are a more Buffy-Brown (Ridgway, 1912) than specimens from Tucumán. The tips of the hairs are particularly light buffy, creating a slightly frosted appearance dorsally. Ventrally, the hairs are very light grayish-tipped, giving a whitish cast to the underparts. The membranes are dark grayish or blackish. Specimens from Tucumán are truly diminutive (Table 1) and are uniquely colored, being bright, glossy brown above, between Auburn and Chestnut of Ridgway (1912). The coloration below is buffy, and the membranes are brownish-black. This population appears to be distinctive, but an adequate assessment of individual and geographic variation cannot yet be made.

In Brazil is a third population, *E. d. diminutus*. These bats are larger than *E. d. fidelis* (Table 1) and are more brownish in color. The only known female of this race approaches the smaller males of *E. f. furinalis* in size (Table 1 and Figs. 1 and 3). The holotype (from São Marcello, Rio Preto, Bahia, Brazil, Osgood, 1920) is similar to the specimens of *E. diminutus fidelis* (Figs. 2 and 3). The specimen from São Paulo is the darkest of this species I have seen, appearing slightly darker and with a more reddish tone than the color Warm Sepia of Ridgway (1912). Its underparts are several shades lighter (with buffy tips to the hairs), and the membranes are blackish. Conversely, the specimen from Maranhão is the lightest brown of the species, between Sanford's Brown and Auburn. The UPGMA analysis places the São Paulo specimen (MCZ 24821) closest to the holotype of *E. d. fidelis* (Fig. 3). In contrast, discriminant function/canonical analysis II places that specimen closest to the *E. diminutus* holotype (Fig. 2, Table 4). In the first discriminant function analysis, this specimen was positioned intermediate to the holotypes of *E. d. diminutus* and *E. d. fidelis* (MCZ 24821 is the uppermost male in the *E. d. diminutus* cluster in Fig. 1). Overall, this specimen appears to be closest to *E. d. diminutus*.

Specimens of *E. diminutus* examined by me are listed below:

*E. diminutus diminutus*.—BRAZIL. Maranhão: Alto Parnabyba (=Parnaíbo), 1♂ (FMNH). Minas Geraes: Lagoa Santa, 1♀ (alc. with skull removed) (FMNH). São Paulo: Furnas do Yporanga, 1♂ (MCZ).

*E. diminutus fidelis*.—ARGENTINA. Tucumán: Aguas Chiquitas, about 800 m, Sierra

de Medina, 1♂ (juvenile), 2♀, + chromosomes (CM). URUGUAY. *Rio Negro*: Arroyo Negro, 15 km S Paysandu, 1♂, 3♀ (AMNH); Quebracho Paysandu, 2♀ (FMNH).

A specimen from Itaté, Corrientes, Argentina (BMNH 24.6.6.4), was not examined by me, but is referable, on the basis of measurements supplied by Mr. Hill, to *E. d. fidelis*. The specimen (BMNH 1.8.1.1) referred to *E. d. dorianus* by Davis (1966), and the specimen (UCONN 15649) assigned to *E. cf. fidelis* by Wetzel and Lovett (1974) are both *E. furinalis*. Two other specimens, which are in the Paris Museum (Museum National D'Histoire Naturelle, Register Nos. 836/631 and 838/642), and which were a part of the type series of *Vespertilio hiliarii* Geoffroy, may be assignable to *E. diminutus* (see Davis, 1966:257).

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#### LITERATURE CITED

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